

## Shifts of Thermogenesis in the Prairie Vole (*Microtus ochrogaster*)

### Strategies for Survival in a Seasonal Environment

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**Summary.** The weight-specific oxygen consumption ( $\dot{V}_{O_2}$ ) of prairie voles caught in winter is 24% higher at 27.5° C and 29% higher at 7.5° C than that of summer animals, thus affording a higher weight-specific thermogenesis in winter than in summer which may allow tolerance to lower thermal exposures. Coincident with the increase in weight-specific rates of oxygen consumption is a decrease in body weight. When total energetic cost to maintain an animal per unit time is calculated, the cost at 27.5° C is the same for both summer and winter animals. Further, the cost to maintain an animal at 7.5° C is less in winter than in summer. Arguments are presented suggesting that prairie voles compensate for increased weight-specific thermogenesis in winter by lowering body weight. The responses to thermal acclimation are quite different in summer and winter animals, thus implying different sorts of metabolic organization. Acclimation to 5° C effects a 26% increase in  $\dot{V}_{O_2}$  at 27.5° C of winter voles, and acclimation to 30° C does not change  $\dot{V}_{O_2}$ . In contrast,  $\dot{V}_{O_2}$  at 27.5° C of summer animals is unaffected by 5° C acclimation, and depressed 20% by 30° C acclimation. Thus, the animals are capable of considerable physiological adjustment to varying thermal conditions in different seasons.

### Introduction

Small, non-hibernating mammals living in north temperate and boreal regions are faced each year with seasonal changes in their thermal environment. Thus, they cannot be adapted to only one extreme or the other, as they may be at a disadvantage when stressed with a contrasting season.

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The responses of small mammals to chronic low temperature stress in laboratory situations (acclimation) have received much attention (see reviews by Barnett and Mount, 1967; Chaffee and Roberts, 1971). In many small mammals one such response is a general increase in thermogenesis. However, wild populations of small mammals are not only exposed to changes in temperature but to a variety of other stimuli, and the manner in which the animals are stressed by temperature in the field may be very different than in laboratories. Animals exposed to such a variety of natural, seasonally changing stimuli are said to be acclimatized (see Folk, 1966, for discussion of terminology) and may show different response patterns to seasonal cold than do animals acclimated to cold. Much less information is available concerning acclimatization responses of small mammals. Heroux (1963) has described the thermogenic responses of winter and summer-caught Norway rats and has shown differences between acclimation and acclimatization responses. Several species of small mammals apparently increase insulation during winter and thus may show decreases in thermogenesis in response to acclimatization rather than the increases shown during low temperature acclimation (see Hart, 1971, for review). However, recently Rosenmann et al. (1975) found seasonal changes in thermogenesis of red-backed voles, *Clethrionomys rutilus* in Alaska. The metabolic turnover rates (Kleiber, 1975) were 18% higher in winter than summer animals.

Furthermore, in recent years ecologists have been concerned with energy flow through various ecosystems and thus with animal energy budgets (see Gesaman, 1973, for review). Such energy budgeted for mammals frequently include modification factors for summer and winter conditions. These modification factors usually involve increasing winter metabolic requirements under the assumptions that: (1) animals will be exposed to lower ambient temperature per se, and (2) because of low temperature exposure they will show an increased thermogenic response due to thermal acclimation (Grodzinski and Gorecki, 1967). However, since animals in the field will be acclimatized there is some concern as to how seasonal corrections should be made for yearly energy budgets (Grodzinski and Wunder, 1975).

Prairie voles, *Microtus ochrogaster*, are found in grassland areas throughout the prairie states of North America from Alberta and Saskatchewan south to Oklahoma and thus inhabit regions which undergo seasonal thermal fluctuations. Therefore, we undertook this study to investigate the effects of acclimatization, acclimation and their interactions on thermogenesis of the prairie vole in order to better understand how the animals have adapted to these contrasting thermal situations and to determine what sorts of adjustments may be necessary when discussing seasonal energy needs.

## Methods

All voles used in this study were captured with Sherman live traps using rolled oats as bait in an area of early grass-forb succession within mountain shrub habitat (Costello, 1954) immediately north of Horsetooth Reservoir 8 km N.W. of Fort Collins, Larimer County, Colorado. Winter animals were captured in 1974 on 21 January and 25-26 February; summer animals were taken

on 5–8 and 19 August. No significant differences in metabolism existed between the two winter groups or the two summer groups and data for each season were combined. In order not to confound results with effects of pregnancy or growth of juveniles, animals weighing less than 30 g and pregnant females were not used.

#### *Weather Data*

In order to get a rough, comparative index of the macroclimatic conditions to which the animals were exposed prior to capture, we analyzed daily temperature data from the Colorado State University Weather Station 8 km S.E. of the trapping area for a 2-week period prior to each trapping session. We used 2 weeks since it takes 10–14 days to demonstrate temperature acclimation effects in the lab (see Hart, 1971, for review). We computed the average daily maximum, minimum and mean for each period. Although this analysis does not tell us the microclimatic conditions to which the animals were exposed in the field, it should allow comparison of the differences between trapping sessions. In winter the area is seldom snow covered and then only for a few days to 1 or 2 weeks at most. Grasses do not die back until late summer or fall.

#### *Experimental Groups*

Upon capture, animals were brought to the laboratory where they were weighed, sexed and placed individually in plastic cages (15 × 12 × 32 cm) with wood shavings. Purina lab chow, rolled oats and water were provided ad libitum. Newly captured voles were maintained at 22–24° C on an irregular photoperiod for not more than 72 h following capture. During this period resting metabolism (RMR) was determined over a range of ambient temperatures (2.0–40.0° C). However, we concentrated our efforts at two test temperatures, 7.5° C for a cold exposure and 27.5° C. At the beginning of the study 27.5° C appeared to be within thermoneutrality for the voles. But inspection of Figure 1 suggests that 27.5° C was not in thermoneutrality for all groups. Hence for comparative purposes we shall simply call these results RMR at 27.5° C or 7.5° C. Following measurements of RMR for animals fresh from the field, the voles were randomly divided into two groups and placed in temperature controlled cabinets ( $\pm 0.5^\circ\text{C}$ ) at either 5 or 30° C for two weeks before RMR determinations were repeated (acclimated animals). Photoperiod in each chamber was held at 12L:12D (0700–1900 MDT). We selected this thinking of it as a “neutral” photoperiod, although it is not and was different from field photoperiods. Thus our temperature acclimation groups, in reality, were also acclimated to a 12L:12D photoperiod. There were six treatment groups: (1) Winter animals from the field, (2) Winter animals acclimated to 5° C, (3) Winter animals acclimated to 30° C, (4) Summer animals from the field, (5) Summer animals acclimated to 5° C, (6) Summer animals acclimated to 30° C.

#### *Oxygen Consumption (RMR)*

Oxygen consumption was determined using an open flow system with a Beckman model G-2 oxygen analyzer. A 3.8 l glass jar and lid, fitted with two ports for air flow and one for insertion of a thermocouple, served as a respirometer. Dry air was pumped through the chamber at a rate of 700 cc/min. Air flow was controlled by Brooks E/C flow meters which had been calibrated with a Brooks Vol-U-Meter flow calibrator. Air passed through columns of “Ascarite” and “Drierite” to remove carbon dioxide and water before being metered into the oxygen analyzer (Condition B of Hill, 1972).

The respirometer was placed in a constant temperature cabinet where ambient temperature could be regulated to within  $\pm 0.1^\circ\text{C}$ . Temperature inside the respirometer was continuously monitored.

Measurements were conducted between 0700 and 1900 h during the animals' simulated daylight hours. Lights inside the temperature cabinet were kept on during each run. Voles were held at an experimental temperature for at least 1 h equilibrium periods prior to recording metabolism. Most determinations took several hours, during which time oxygen concentration of air from

each respirometer was recorded for 5 min every 10 min. An average of the lowest of these recordings was used in RMR calculations all of which are expressed as STP conditions.

Body temperature ( $T_B$ ) was measured prior to and after each metabolism determination with a thermocouple (20 ga, Thermo-Electric Co.) inserted 3 cm into the rectum and recorded on a Honeywell recording potentiometer.

### *Statistical Analyses*

Statistical comparisons among treatment groups were made using analysis of variance. Homogeneity of variance in such comparisons was checked by Bartlett's test. Individual comparisons were made using *t*-tests. Calculations and statistical tests were run using computer programs developed by the CSU Statistical Services Laboratory.

## **Results**

### *Weather Data*

There were no differences ( $P > 0.05$ ) in any of the daily temperature means between the January and February trapping sessions. Average daily mean temperature was around  $+1.2$  to  $-2.6^\circ\text{C}$  and average daily minimum temperature was  $-6.7$  to  $-10.1^\circ\text{C}$ . There was a very significant difference between winter temperature means and summer temperatures where average daily mean temperature was  $+20.5^\circ\text{C}$  and average daily maximum temperature was  $27.9^\circ\text{C}$  (Table 1).

### *Body Weight*

Associated with the different experimental treatment groups are some differences in body weight ( $P < 0.05$ ). The winter field animals and winter animals acclimated to  $5^\circ\text{C}$  are not different in body weight from each other but both groups are lighter than any of the other treatment groups. None of the other treatment groups differ in weight among each other (Table 2).

**Table 1.** Temperature data for trapping periods<sup>a</sup>

Period	Maximum	Minimum	Average
7-20 January 1974	+4.9 ± 8.9	-10.1 ± 8.7	-2.6 ± 8.6
11-24 February 1974	+9.1 ± 4.2	-6.7 ± 2.3	+1.2 ± 2.2
22 July-4 August 1974	+27.9 ± 3.4	+13.1 ± 2.3	+20.5 ± 2.4

<sup>a</sup> Values given are daily temperature means  $\pm 1$  S.D. in degrees C. See "Methods" for data acquisition

**Table 2.** Metabolic rate of prairie voles at 27.5° C<sup>a</sup>

Treatment	Body weight	ccO <sub>2</sub> /g·h	Predicted metabolism <sup>b</sup>	% Deviation from predicted	ccO <sub>2</sub> /g <sup>0.75</sup> ·h <sup>c</sup>
Winter field	38.5 ± 4.5 (15)	2.16 ± 0.34 (15)	1.53	+ 41	5.37 ± 0.86 (15)
Winter 5°	41.0 ± 5.6 (8)	2.72 ± 0.40 (8)	1.50	+ 81	6.85 ± 0.89 (8)
Winter 30°	48.4 ± 8.9 (10)	2.19 ± 0.25 (10)	1.44	+ 52	5.75 ± 0.63 (10)
Summer field	47.4 ± 8.9 (9)	1.74 ± 0.20 (9)	1.45	+ 20	4.53 ± 0.33 (9)
Summer 5°	50.0 ± 4.7 (11)	1.76 ± 0.12 (11)	1.43	+ 23	4.67 ± 0.30 (11)
Summer 30°	48.5 ± 8.7 (10)	1.40 ± 0.15 (10)	1.44	0	3.68 ± 0.36 (10)

<sup>a</sup> Values given are means ± 1 S.D. Numbers in parentheses are sample sizes

<sup>b</sup> The following equation was used to estimate metabolism:  $ccO_2/g/h = 3.8 W^{-0.25}$  (modified from Morrison et al., 1959)

<sup>c</sup> ccO<sub>2</sub>/body weight raised to the 0.75 power/h

Hart (1971, pp. 36–38) has suggested that when comparing metabolic data from treatment groups with animals of different weights, it is important to correct for the effects of size differences before attempting to interpret the effects of treatment differences. To do this he suggests expressing the metabolic results as a function of weight raised to some exponential power, that exponent being dependent upon the relationship between weight and metabolism for the particular species under study. Since we do not know of any good data correlating body size with resting metabolism in prairie voles, we used the general exponent for mammals (0.75) for such comparisons. When the data are expressed in this fashion our overall conclusions from group comparisons do not differ significantly from those conclusions based upon data expressed simply as metabolism per unit weight.

### *Energy Metabolism*

The oxygen consumption of animals measured at 27.5° C show that there is a definite shift in metabolism ( $P < 0.05$ ) of animals between different seasons and as a result of thermal acclimation. During the winter the weight-specific metabolism of newly captured voles is 24% greater than that of animals caught in the summer (Table 2). In addition to comparing the two metabolic values we can compare the values with the “expected” metabolism for a mammal of the weight for each group using an allometric relationship modified from Morrison, Ryser and Dawe (1959). With this comparison, metabolism of winter

**Table 3.** Metabolic rate of prairie voles at 7.5° C<sup>a</sup>

Treatment	Body weight	ccO <sub>2</sub> /g·h	ccO <sub>2</sub> /g <sup>0.75</sup> ·h <sup>b</sup>
Winter field	36.3 ± 4.2 (9)	4.44 ± 0.52 (9)	10.87 ± 1.11 (9)
Winter 5°	40.5 ± 6.9 (7)	4.28 ± 0.34 (7)	10.75 ± 0.75 (7)
Winter 30°	44.9 ± 8.2 (8)	4.10 ± 0.43 (8)	10.76 ± 0.85 (8)
Summer field	50.0 ± 5.5 (13)	3.45 ± 0.28 (13)	9.17 ± 0.64 (13)
Summer 5°	48.5 ± 5.9 (9)	3.22 ± 0.42 (9)	8.49 ± 1.05 (9)
Summer 30°	47.3 ± 8.4 (8)	3.27 ± 0.32 (8)	8.55 ± 0.61 (8)

<sup>a</sup> Values given are means ± 1 S.D. Numbers in parentheses are sample sizes

<sup>b</sup> ccO<sub>2</sub>/body weight raised to the 0.75 power/h

field animals is 41% higher than predicted and summer field animals only 20% higher (Table 2). Thus, winter animals not only have higher metabolism than summer animals but have even higher metabolism on an allometric basis.

There is a dramatic difference in the responses at 27.5° C of winter and summer animals to thermal acclimation. Winter animals acclimated to cold show a 25% increase in weight-specific metabolism but when acclimated to warm temperature there is no difference from field animals (Table 2). Summer animals show a different response pattern to thermal acclimation. When acclimated to cold, summer voles, unlike winter voles, show no differences in metabolism from field animals. Further, when acclimated to warm temperature summer animals show a 20% decrease ( $P < 0.05$ ) in metabolism when compared to field animals and have a metabolic rate which agrees with the allometric prediction (Table 2).

Metabolic responses of animals tested at an ambient temperature of 7.5° C show somewhat different patterns among the treatment groups than the responses at 27.5° C. There are no significant differences in weight-specific metabolism among the treatments within either winter or summer animals. However, there is a significant ( $P < 0.05$ ) difference between responses of the winter groups of voles compared to the summer groups with winter animals having higher metabolic rates (Table 3 and Fig. 1).

### Body Temperature

At 27.5° C there are no differences ( $P < 0.05$ ) in the level of  $T_B$  between summer and winter field animals (Table 4). Nor are there differences in  $T_B$  between field animals tested at 7.5° C. However, in both summer and winter the field

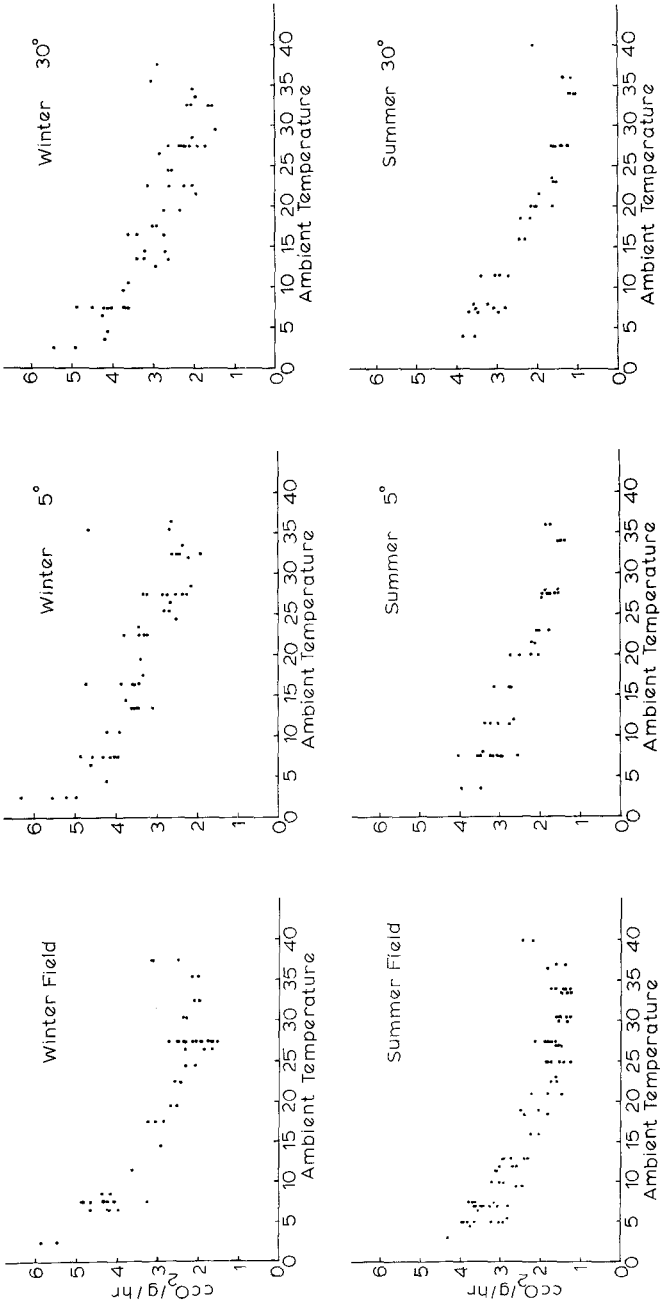


Fig. 1. Weight-specific oxygen consumption of prairie voles captured during different seasons and acclimated to different thermal regimes as a function of air temperature (°C)

**Table 4.** Body temperature of prairie voles<sup>a</sup>

Treatment	Ambient temperature	
	27.5° C	7.5° C
Winter field	37.8 ±0.5 (15)	37.3 ±0.7 (9)
Winter 5°	38.1 ±0.6 (8)	38.1 ±0.4 (7)
Winter 30°	38.3 ±0.5 (11)	38.1 ±0.8 (9)
Summer field	37.8 ±0.6 (9)	37.1 ±0.8 (15)
Summer 5°	38.5 ±0.7 (11)	37.6 ±0.7 (9)
Summer 30°	38.4 ±0.3 (10)	37.6 ±0.8 (8)

<sup>a</sup> Values given are means ± 1 S.D.  
Values in parentheses are sample sizes

animals have a lower  $T_B$  at 7.5° C than at 27.5° C ( $P < 0.05$ ). There are no differences in  $T_B$  of winter animals from either acclimation group under any  $T_A$  condition and both acclimation groups regulate  $T_B$  at the same level as field animals when tested at 27.5° C. Thus winter acclimation groups are regulating  $T_B$  at higher levels than field animals when exposed to low test temperatures but are not doing so at 27.5° C. In contrast to this, both summer acclimation groups regulate  $T_B$  higher than field animals at  $T_A$  of 27.5° C and in all cases regulate  $T_B$  lower at 7.5° C than at 27.5° C (Table 4). These lower  $T_B$  levels of acclimated animals at 7.5° C exposures are the same as the  $T_B$  for winter field animals at 7.5° C exposures. Thus summer acclimation groups of voles regulate at lower  $T_B$  levels when exposed to low temperature than do winter acclimation groups.

## Discussion

It has previously been stated that many microtine rodents have basal metabolic rates ( $BMR$ ) which are considerably (75%) higher than those predicted by allometric relationships (Packard, 1968; Hart, 1971, for review). Packard (1968) suggested that since the subfamily Microtinae evolved in boreal regions, it is reasonable to postulate that these high metabolic rates are adaptive to allow for increased thermogenesis during acute low temperature stress. Thus the high  $BMR$ 's are the consequence of an upward shift in maximum metabolism. Obviously, this is an energetically expensive adaptation. In order to have high thermogenic capacity primarily for winter low temperature stress, the animals must



have *high* energetic turnover all year. Results of our study indicate that *M. ochrogaster* does not maintain these high metabolic rates all year but shows varied responses to different seasons and these resting rates can be further modified by thermal acclimation (Table 2). Further, the metabolic rate of *M. ochrogaster* at 27.5° C is only 20–40% greater than that predicted by allometry (Table 1) not 70–80% as previously suggested for microtines in general (Packard, 1968). Admittedly, our results are not true “basal” metabolism but, if anything, that should make them higher not lower than predictions. Inspection of previous investigators’ methods suggests that in many instances they were measuring rates of winter animals acclimated to low temperatures in the lab (animals were held for several weeks at low  $T_A$  in the lab) not true field rates. Thus when calculating yearly energy budgets for microtines based on allometric models (Grodzinski and Wunder, 1975; Wunder, 1975) the previously suggested modification of a 75% increase should not be used. Further study is needed on other microtines to determine just how this group may vary from allometric models.

As mentioned in the Introduction and indicated by our weather data, prairie voles in Colorado inhabit areas which seasonally present contrasting thermal environments. Although the animals are most often active below a dead grass mat, the areas are seldom snow covered and hence the animals are exposed to changes in air temperature.

It is important to note that there are two aspects of metabolism which are important for small mammals exposed to cold and these two are not always clearly delineated. First, the animals need enough insulative and/or thermogenic capability to withstand low temperature exposure without becoming pathologically hypothermic. Scholander (1955) and others have pointed out that it is not possible to greatly increase the insulation on small mammals. Instead they must cope with cold stress by behavioral avoidance and/or increased thermogenic capacity (ability to produce heat); that is, they must meet their thermoregulatory needs. In this regard it is important that we examine metabolism per unit weight of animal (cal/g·time) since metabolic data expressed in this fashion indicate the *rate* at which an animal can turn over energy and such *rates* are important to combat cooling environments. This expression indicates degree of thermogenesis. Kleiber (1975) has suggested calling this expression “metabolic turnover rate” (*MTR*) and indicates that it “...can mean the turnover rate of chemical energy in an animal’s body.” Secondly, in order for an animal to exist it must be able to meet its total caloric needs for a given circumstance or starve, lose weight and possibly die. To consider energy needs of animals in this light it is important to express data as cal/animal·time. To meet these needs animals must be able to gather, consume and assimilate enough energy to maintain themselves. To exist in cold both of the needs discussed above must be met. An animal must be able to turn energy over and produce heat fast enough to meet its thermoregulatory needs or it will cool, and it must be able to gather and assimilate the total number of calories needed to maintain itself intact or starve.

If we assume that, in general, voles are exposed to lower temperatures and greater cold thermal stress in winter than in summer, it seems reasonable

to assume that the shift to higher levels of *MTR* in winter (25% greater than summer) is related to adjusting thermoregulatory capabilities to meet these cold stresses just as Packard (1968) suggested that high BMR, in general, not seasonally, reflects such increased capabilities. Although we were unable to test voles at  $T_A$  low enough to elicit maximal *MTR*, Rosenmann et al. (1975) recently showed that higher winter *MTR*'s at thermal neutral temperatures are associated with higher maximal *MTR* in red-backed voles (*Clethrionomys rutilus*). These seasonal changes in thermogenesis are similar to the responses of white-footed mice (*Peromyscus leucopus*) demonstrated by Lynch (1973), but different from larger animals such as the arctic hare. In these larger forms, found in a continuously cooler habitat, insulation is increased to combat heat loss and *MTR* may be low (Wang et al., 1973).

Obviously if *MTR* is increased by 25% in winter for thermoregulation, then the total caloric requirements for a winter vole would be 25% greater than a summer vole in a similar thermal environment, provided the animals are of the same weight. If foraging and assimilation efficiencies remain the same, then presumably voles would need to be out foraging in a colder environment and be exposed to predators for 25% more time in winter than in summer. We know nothing about foraging efficiencies, however, we do know that food quality probably changes seasonally. Uresk and Sims (1975) found that the nitrogen content of green, growing grasses was several times greater than in standing dead (winter) material. Presumably voles process their food with gut microflora similar to ungulate grazers and nitrogen is necessary for efficient "rumination." When nitrogen content is low, assimilation efficiency decreases in small mammals (Grodzinski and Wunder, 1975). And, indeed, Cherry and Verner (1975) recently found that assimilation efficiency is significantly decreased in winter prairie voles in Illinois. Thus the voles would have to spend even greater time foraging in winter.

However in association with the increase in *MTR* we found that the winter voles weighed less than summer voles (Table 2). Therefore it should take fewer calories to maintain them than if they held to the higher summer weights. To investigate this we calculated caloric requirements to maintain an animal/hr at 27.5° C and 7.5° C in summer and winter. Our results showed that the cost to maintain an animal at 27.5° C is the same ( $P > 0.05$ ) in winter as in summer (Table 5). Even more surprising is the comparison at 7.5° C. It costs less ( $P < 0.05$ ) to maintain winter animals at this lower temperature than to maintain summer animals. Thus it appears that the shift in body weight can compensate or more than compensate total energetics for changes in *MTR* thermogenesis.

It might be argued at this point that the changes in thermogenesis which we report are not real differences in thermogenic level of metabolic tissue but are simply the result of changes in fat content of voles which contribute to the denominator in an *MTR* calculation (this would require high fat content in summer and low in winter). Although we cannot entirely discount that possibility, we feel the *MTR* values reflect actual seasonal changes in level of heat production for the following reasons. First, Wunder (unpubl. obs.) inspected carcasses of animals caught during summer 1975 and winter 1976 at the same place as those used in this study. Summer animals showed no subcutaneous

**Table 5.** Caloric needs of prairie voles<sup>a</sup>

Treatment	Exposure temperature	
	27.5° C	7.5° C
Winter field	398.4 ± 76.8 (15)	768 ± 76.8 (9)
Summer field	388.8 ± 43.2 (9)	830.4 ± 72.0 (13)

<sup>a</sup> Units are cal/animal/h. Values given are means ± 1 S.D. Numbers in parentheses are sample size

or intraperitoneal white fat deposits and winter animals had some deposits. These observations are similar to those of Didow and Hayward (1969) who found that *Microtus pennsylvanicus* in Canada had higher levels of both brown and white fat in winter.

It might also be argued that the reason winter voles weigh less than summer voles is because they are, on the average, younger voles. Although we cannot discount this possibility several studies have shown winter decreases in other small mammals (Rosenmann et al., 1975; Whitney, 1973; Fuller, 1969) and in shrews these decreases are in all body dimensions (Dehnel, 1945; Mezhzherin and Melnikova, 1966). Recently, Iverson and Turner (1974) reported a seasonal pattern of a decrease in body weight for individual *Microtus pennsylvanicus*, the meadow vole, during the winter over a several year period in Manitoba. Iverson and Turner (1974) also reported several other studies showing similar results with other microtines. They suggest that the advantage of such a weight shift would be to decrease total caloric needs for a vole and thus the amount of time the animals would need to get out of a nest to forage. However, Iverson and Turner did not look at actual metabolic costs. In contrast to their hypothesis, our results suggest that if the animals spend much time in thermal neutrality (an insulated nest) they will not necessarily have decreased total caloric needs but may have similar needs to summer. Indeed, although it is difficult to interpret results because of thermal acclimation procedures, Cherry and Verner (1975) found that ingestion energy (food consumed) is the same for summer and winter prairie voles from Illinois tested in the lab. They also found that existence energy (energy ingested minus that lost in feces and urine during a time of no production) is lower in winter animals but this could be due to a reduction in activity of animals in cages on shorter photoperiods. However, they did not study thermoregulation in their animals and do not know what the level of *MTR* was. Further, the body weights of their animals did not show the seasonal changes which we found. They also measured seasonal increases in hair length and density of their animals. However, when they measured thermal conductance (this may be thought of as the inverse of insulation) of vole carcasses, they found no statistically significant decrease in winter, the value for both seasons (0.73 cal/g · h · °C) being about that predicted on the basis of allometry (Herreid and Kessel, 1967). Thermal conductance may also be calculated from metabolic data using the formula  $C = MTR / (T_B - T_A)$  (see Bartholomew, 1972, for discussion). We made such calculations for our

**Table 6.** Thermal conductance of voles at 7.5° C

Treatment	Thermal conductance cal/g/h/° C
Winter field	0.71 ± 0.03 (8)
Winter 5°	0.67 ± 0.02 (7)
Winter 30°	0.65 ± 0.02 (8)
Summer field	0.56 ± 0.01 (13)
Summer 5°	0.51 ± 0.02 (9)
Summer 30°	0.52 ± 0.02 (8)

study animals exposed to 7.5° C and found that values for winter animals were similar to results of Cherry and Verner (1975); however, values for summer animals were significantly lower (Table 6). Thus the thermal conductance of Colorado prairie voles, during winter with high *MTR*, is about that expected on the basis of allometry. However summer animals have significantly ( $P < 0.05$ ) lower thermal conductance. This seems a paradox and is difficult to resolve. However, thermal conductance is a simplified expression for a variety of heat exchange parameters. With higher winter *MTR*'s animals may lose relatively more heat by respiratory evaporation and convection than summer animals. It has been reported that many small mammals have increased hair density and length in winter (Sealander, 1951, 1972; Khateeb and Johnson, 1971; Borowski, 1958) which should increase insulation. We have no such data for our voles, but if such occurs, the increase in insulation due to hair may be hidden by increases in heat loss parameters (associated with respiration?).

It is more difficult to resolve other differences between our results and those of Cherry and Verner (1975). However, there are some possible explanations. In part, different techniques were used. We studied steady-state metabolic rate phenomena whereas their animals could show different behaviors in metabolic cages which could affect seasonal food consumption. They used carcasses for thermal conductance measurements which does not account for postural, circulatory or respiratory variation which would affect thermal conductance when calculated from metabolic data. Also the winters in Colorado and Illinois may place different stresses on these populations. And, lastly, vole populations are cyclic and some differences in our studies may be related to differences in phase of the cycle from which animals were taken. The second fall (1975) following our study the population we studied crashed.

Our acclimation study suggests that when faced with colder environments winter prairie voles are capable of even greater thermogenic increases than those shown by field animals. However, it has frequently been questioned whether low temperature acclimation as demonstrated in the laboratory (usually 24h per day exposure to low temperature, as in our study) has relevance to animals in the field which are exposed to a mosaic of temperatures. Although we cannot answer this question directly, our results and those of Lynch (1973) and Rosenmann et al. (1975) demonstrating an increase in thermogenesis in winter animals suggest that low temperature exposures in the field can effect

increased thermogenesis. Winter animals should be exposed to a mosaic of temperatures lower than those found in summer. Also, Heldmaier (1975) has shown that the amount of brown fat (associated with the non-shivering thermogenic response of small mammals) deposited by house mice is directly related to the temperature of exposure. He has also shown that an identical response can be elicited by exposing mice held at 30° C to low temperatures for as little as 2.5 h each day. Thus it is possible that voles exposed to lower and lower temperature mosaics in the field may show increased low temperature tolerance responses similar to those shown in response to low temperature acclimation in the lab. Indeed, Lynch (1973) found increased brown fat deposition and increased non-shivering thermogenic responses in white-footed mice following the first cold exposures in the fall with increases in response levels into the winter. Rosenmann et al. (1975) found similar changes in red-backed voles in Alaska.

That the voles adjust metabolically to different seasons is clearly shown by results of our acclimation studies. Winter animals shift to higher *MTR*'s when cold acclimated and show no change when acclimated to high (30° C) temperature. This contrasts to the lack of change upon low temperature acclimation of summer animals and depression in *MTR* with high temperature acclimation. Obviously if it is adaptive to have high *MTR* during the winter it would not be of advantage to shift back down to low *MTR* levels in response to warm spells in the middle of winter as often occur in Northcentral Colorado for the return to snow and cold weather can occur rapidly. Likewise we find that prairie voles are operating in the field at lower *MTR* in summer than winter at all temperatures tested. This seasonal reduction is similar to that shown for white-footed mice (Lynch, 1973) and for desert cottontails (Hinds, 1973). Further, our temperature acclimation study shows that with high temperature exposure, summer prairie voles can effect an even greater (another 20%) depression in *MTR* at 27.5° C. Thus the voles are able to respond to increases in environmental thermal stress by reducing rates of heat production. However, presumably in the field they would not increase *MTR* in response to cold periods during the normally warm portion of the year. Thus there must be some cue (such as nutritional changes in food, etc.) other than temperature for modulating thermal acclimation responses.

Body temperature responses of animals in the various treatment groups also vary and suggest that although the responses of both summer and winter field animals are similar, the underlying mechanisms vary seasonally. Both field groups regulate  $T_B$  at 37.8° C when exposed to 27.5° C and significantly ( $P < 0.05$ ) drop  $T_B$  when exposed to 7.5° C. All acclimation groups regulate  $T_B$  at similar levels when exposed to 27.5° C and this level is significantly higher than field animals (Table 4). However, when exposed to moderate cold (7.5° C) the response patterns vary. Winter acclimation groups regulate at the same  $T_B$  as at 27.5° C, thus higher than field animals. Conversely, summer acclimation groups show lower ( $P < 0.05$ )  $T_B$ 's at 7.5° C than at 27.5° C the same as field animals. These results suggest that the animals cope with moderate cold differently in different seasons. In summer, insulation, as represented by  $1/C$ , may be the main means of meeting cold stress. This is, of course, in

part tied to the larger body size. In most instances insulation will suffice to meet most summer cold stress since these should be moderate relative to winter. However, in winter at the lowest temperature stresses insulation alone may not suffice to combat heat loss; thus the animals have increased levels of thermogenesis (as demonstrated by Rosenmann et al., 1975, and our *MTR* increases) and when the animals are well fed as in the lab they maintain high  $T_B$  as a result of this high *MTR* turnover.

One last point bears discussion. Comparison of our results and those of Rosenmann et al. (1975) to the results of Lynch (1973) suggest some interesting interactions between thermoregulation, energetics and feeding strategies. Voles are primarily grazers (grass feeders) and although food quantity may not vary greatly seasonally, quality does as discussed above, and without preparation (such as drying) grass cannot be stored. White-footed mice are primarily seed eaters. Seasonally the quantity of seed production varies but once a seed is produced its quality should be constant and seeds can readily be stored. Both groups of animals shift to higher *MTR* in winter than summer (Lynch, 1973), presumably for thermoregulation at the lowest  $T_A$  exposures. Such shifts would demand higher total energy needs for winter animals over summer animals even if exposed to similar thermal environments and activity schedules. Voles appear to shift to lower weights in winter which helps compensate so that energy costs are similar or slightly less to maintain individuals at moderate ( $7.5^\circ\text{C}$ ) cold. Lynch (1973) did not find such a weight change in white-footed mice. This suggests that energetic costs for similar thermal conditions are higher for winter than summer mice. Barry (1974) has recently found that several species of *Peromyscus* hoard seeds and the amount of seeds cached is related to photoperiod and temperature. The northern subspecies of *Peromyscus maniculatus* and *P. leucopus* cache most seeds under conditions of short days and low temperature. Therefore these animals show a different adaptive pattern from voles whereby they may prepare for higher energy demands by storing energy and, thus, may also reduce foraging activity during coldest conditions. In addition, if they run short of energy, white-footed mice have been shown to be capable of torpor (Morhardt and Hudson, 1966; Morhardt, 1970; Hill, 1975) whereas this facility has never been shown in voles and they would have to continue to forage in coldest conditions.

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